herbivores [12]. We agree that abiotic gradients are important determinants of biogeographic patterns. However, we suggest temperature as an alternative to soil fertility because it is not dependent on herbivory and decomposition rates and has direct impacts on the distribution, activity, and metabolic rate of organisms. Consequently, the niches of the degradation agents and ecosystem-level patterns in recycling pathways will be better captured by temperature than soil fertility.

Research Directions

While we have criticised aspects of Pausas and Bond's proposed framework, we recognise the value of their holistic approach toward characterising the biogeography of differing recycling pathways. We suggest that applying these ideas to more accurate and representative recycling conceptual models that are built upon the large body of literature exploring these themes (e.g., Figure 1) [2,4,10,12] is a productive way forward. Further, to be truly holistic, no ecological framework can omit invertebrates. Finally, rather than contrasting wildfire, herbivory, and decomposition, it would be more useful to focus on the relative dominance of the different agents of recycling that are acting on the same type of material. For example, in a given ecosystem, how much live plant matter is consumed separately by vertebrate and invertebrate herbivores? How much dead plant material is decomposed separately by invertebrate and microbial decomposers? Only with these data can we understand the changing dominance of different mediators of carbon and nutrient recycling across biogeography. Experimental approaches both within and across biomes will be needed to determine these numbers (e.g., [7,9]), together with the abandonment of the traditional taxonomic and geographic silos in which many researchers operate. This ecosystem-level, experimental macroecological approach will allow us to map the changing dominance of different recycling agents across space and time.

[1]Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, L69 3GP, UK
[2]Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa
[3]School of Biological Sciences, The University of Hong Kong, Hong Kong, SAR, China
[4]Department of Life Sciences, Natural History Museum, London, UK
[5]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa
[6]These authors are joint first authors

*Correspondence:
T.R.Bishop@liverpool.ac.uk (T.R. Bishop) and
Hannah.griffiths@liverpool.ac.uk (H.M. Griffiths).
[@]Twitter: @HanMGriffiths (H.M. Griffiths) and @TomRBishop (T.R. Bishop).
https://doi.org/10.1016/j.tree.2020.09.005

References

1. Pausas, J.G. and Bond, W.J. (2020) On the three major recycling pathways in terrestrial ecosystems. *Trends Ecol. Evol.* 35, 767–775
2. Barton, P.S. *et al.* (2019) Towards quantifying carrion biomass in ecosystems. *Trends Ecol. Evol.* 34, 950–961
3. van Klink, R. *et al.* (2020) Rewilding with large herbivores: positive direct and delayed effects of carrion on plant and arthropod communities. *PLoS One* 22, 1–17
4. Swift, M.J. *et al.* (1979) *Decomposition in Terrestrial Ecosystems*, University of California Press
5. Bar-On, Y.M. *et al.* (2018) The biomass distribution on Earth. *Proc. Natl. Acad. Sci. U. S. A.* 115, 6506–6511
6. Crowther, T.W. *et al.* (2019) The global soil community and its influence on biogeochemistry. *Science* 365, 1–10
7. Griffiths, H.M. *et al.* (2019) Termites can decompose more than half of deadwood in tropical rainforest. *Curr. Biol.* 29, 118–119
8. Veldhuis, M.P. *et al.* (2017) Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology* 98, 467–477
9. Davies, A.B. *et al.* (2016) Seasonal variation in the relative dominance of herbivore guilds in an African savanna. *Ecology* 97, 1618–1624
10. Metcalfe, D.B. *et al.* (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecol. Lett.* 17, 324–332
11. Kristensen, J. *et al.* (2019) Below-ground responses to insect herbivory in ecosystems with woody plant canopies: a meta-analysis. *J. Ecol.* 108, 917–930
12. Veldhuis, M.P. *et al.* (2018) Ecological autocatalysis: a central principle in ecosystem organization? *Ecol. Monogr.* 88, 304–319

Letter

On the Scale of the Terrestrial Recycling Pathways

Juli G. Pausas [1,*,@] and William J. Bond [2,3]

'No description of the variability and predictability of the environment makes sense without reference to the particular range of scales that are relevant to the organism or processes.'

[(Levin 1992)]

We recently suggested that the main recycling pathways of organic matter and nutrients in terrestrial ecosystems are: microbial decomposition, vertebrate herbivory, and wildfires [1]. By doing so, we provided a new holistic approach of recycling pathways in terrestrial ecosystems. And new research is providing further clues on the interaction among the three pathways [2,3]. Recently, Bishop *et al.* [4] raised three concerns to our approach; here we are responding to each one.

Are Herbivory and Decomposition Part of the Same Biotic Degradation Pathway?

One of the main distinctions among the proposed three pathways was that each one is dominated by a very different actor (vertebrates, microbes, or fire) that perform recycling at different spatial scales (see Table 1 in [1] for additional differences). The microbial pathway acts at small scales (cm to m); the herbivore pathway moves nutrients at intermediate scales (m to km); and the wildfire pathway acts on a broader scale (continental to global). Each of the three pathways includes different steps and is more complex than their short names suggest. For instance, in the herbivore pathway, there are microbes (*Archaea*) degrading organic matter in the guts of the herbivores, and other microbes in the soil degrading the herbivores' wastes. However, thanks to the herbivores, the organic matter in this pathway is moved further than in the microbial pathway.

Traditional studies of nutrient recycling rarely consider herbivory and wildfires, probably because of the problems associated with working at large scales. Our intention is to place the different recycling pathways into the context of the scale of the investigation. By separating microbial decomposition from the herbivore and wildfire pathways, we encourage investigating the transfer of nutrients to locations distant to the original plant source; this large-scale research is promising for the understanding of the functioning of our biosphere [5–7]. Incorporation of plant matter from distant sources can be seen as analogous to aquatic ecology and the cycling of nutrients from within the river or lake system (autochthonous) versus external, terrestrial sources (allochthonous). So, in our opinion, it is important to avoid mixing processes that act at different scales [8].

Does the Inclusion of Invertebrates Facilitate the Distinction of Ecological Scales and Niches?

There are many soil invertebrates that degrade the organic matter at a local scale (smaller than most vertebrates), and thus invertebrates are included (and not omitted) as part of the microbial pathway [1]. However, it is true that invertebrates can generate a recycling pathway of their own, and can act at scales intermediate between the microbial pathway and the vertebrate pathway. Thus, we agree with Bishop *et al.* that incorporating an invertebrate pathway, and characterizing it appropriately, might improve our model.

Even though we did not quantify the importance of each of the three pathways, it is true that our approach may suggest that vertebrates and wildfires are more important than invertebrates in the structure and biogeochemical cycles of plant communities. Certainly, there is some evidence for this. In recent decades, there has been a large amount of information showing that wildfires and/or vertebrate herbivory are the main plant consumers (and C recyclers) across many ecosystems worldwide [9,10], with millions of years of history. Most grasslands and savannas across the world are (and have been) maintained by wildfires and/or vertebrate herbivory. The elimination of these two processes (without excluding invertebrates) has led to huge vegetation changes, converting those low-biomass ecosystems into dense high-biomass forests. Thus, at the global scale, the recycling of matter and nutrients by vertebrates is likely more relevant than by invertebrates; but further research is needed to quantify of the relative importance of each pathway.

Is Temperature a Better Predictor for Recycling Pathways Than Soil Fertility?

We suggested that each pathway has its own niche, with important overlapping areas, and proposed that the main niche axes were water availability and soil fertility [1]. Bishop *et al.* have suggested that soil fertility is not an appropriate niche dimension because it is influenced by the vegetation, and proposed the use of temperature. However, temperature is a poor predictor of the nutrient cycling by fire since fire regularly burns systems from the boreal to the tropics (with more intense fires where they are less frequent). Similarly, mammal herbivory can also change in intensity from boreal regions to the tropics. Soil fertility does indeed tend to be correlated with fire and or mammal herbivory. Flammable vegetation that burns regularly is common on nutrient poor substrates [11] and vertebrate herbivory is common on nutrient-rich substrates [12]. In addition, the recycling pathway by fire tends to deplete nutrients from soils, while vertebrate herbivory tends to enrich soils with nutrients. This adds the important dimension of feedbacks between the soil, the dominant consumer, and the vegetation. So there is no evidence that temperature explains the distribution of the recycling pathways better than soil fertility and water availability.

Conclusion

A novelty of our approach on the terrestrial recycling pathways is that it highlights one of the most important topics in ecology (if not in all of science): the scale; that is, it provides a model that explicitly sets the scale at which organic matter and nutrients are recycled and redistributed. By doing so, we also emphasize the key role of herbivores and wildfires in the global biogeochemical cycles; the role of these plant consumers has been underconsidered in most ecological literature where the microbial pathway is the dominant recycling paradigm.

[1]Centro de Investigaciones sobre Desertificación (CIDE-CSIC), Valencia, Spain
[2]Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[3]South African Environmental Observation Network, National Research Foundation, Claremont, South Africa

*Correspondence:
juli.g.pausas@ext.uv.es juli.g.pausas@csic.es (J.G. Pausas).
[@]Twitter: @jgpausas (J.G. Pausas).
https://doi.org/10.1016/j.tree.2020.10.013

References

1. Pausas, J.G. and Bond, W. (2020) On the three major recycling pathways in terrestrial ecosystems. *Trends Ecol. Evol.* 35, 767–775
2. Leroux, S.J. *et al.* (2020) Herbivore impacts on carbon cycling in boreal forests. *Trends Ecol. Evol.* 35, 1001–1010
3. Carpenter, D.O. *et al.* (2020) Benefit or liability? The ectomycorrhizal association may undermine tree adaptations to fire after long-term fire exclusion. *Ecosystems* Published online October 9, 2020. https://doi.org/10.1007/s10021-020-00568-7
4. Bishop, T.R. *et al.* (2020) Clarifying terrestrial recycling pathways. *Trends Ecol. Evol.* Published online October 1, 2020. https://doi.org/10.1016/j.tree.2020.09.005
5. Doughty, C.E. (2017) Herbivores increase the global availability of nutrients over millions of years. *Nat. Ecol. Evol.* 1, 1820–1827
6. Barkley, A.E. *et al.* (2019) African biomass burning is a substantial source of phosphorus deposition to the Amazon, Tropical Atlantic Ocean, and Southern Ocean. *Proc. Natl. Acad. Sci. U. S. A.* 116, 16216–16221
7. Schoelynck, J. *et al.* (2019) Hippos (*Hippopotamus amphibius*): the animal silicon pump. *Sci. Adv.* 5, eaav0395
8. Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73, 1943–1967
9. Bond, W.J. (2019) *Open Ecosystems: Ecology and Evolution Beyond the Forest Edge*, Oxford University Press
10. Pausas, J.G. and Bond, W.J. (2020) Alternative biome states in terrestrial ecosystems. *Trends Plant Sci.* 25, 250–263
11. Orians, G.H. and Milewski, A.V. (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biol. Rev.* 82, 393–423
12. Archibald, S. and Hempson, G.P. (2016) Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philos. Trans. R. Soc. B* 371, 20150309